CONTRIBUTIONS TO THE LIFE HISTORIES OF PLANTS. No. IV.

BY THOMAS MEEHAN.

On Secund Inflorescence. So far as the author of this paper knows, no explanation has been given as to why flowers are often secund on the rachis. Sachs goes into the subject somewhat (Text Book of Botany, English Ed., p. 189), but evidently without being clear in his own mind as to the proper method of accounting for it, under the prevalent conceptions of phyllotaxis.

To those who have been able to examine many species of the thick-stemmed Begonias, to which this author refers as having leaves from one side of the stems only, it must be evident that they are but herbaceous species that have learned to become erect. What are thickened, creeping rhizomes in some species, have become ascending upright stems in these shrubby ones; and they have carried along in this evolutionary movement the unilateral character of producing the foliage, which must of necessity prevail in a procumbent stem.

This change of the horizontal to the erect position is apparent in many plants, especially in ferns. Tree ferns have no rhizomes, because the trunk of the tree fern is itself but an erect rhizome. In draining old swamps, the author has taken out old rhizomes of *Osmunda regalis*, many feet in length, and three inches in diameter, in no way differing from the trunks of the smaller arborescent ferns except a vertical tendency in the remains of the stipes. There are instances on record where this fern has become wholly arborescent,—that is to say, instead of producing the usual creeping rhizoma, the rhizome has become erect. But whether that rhizome, when erect, continued the lateral arrangement of its former position, as in the allied case of *Begonia*, it did not seem to occur to the observer to note. Again, there is no difference in character between the thick underground rhizome of *Yucca filamentosa* (which never has an erect stem) from the erect stems of its allies (*Y. aloifolia*, *Y. gloriosa*, &c.) which have no creeeping rhizomas. That the latter are but herbaceous species that have learned to elevate their rhizomes while assuming other characters, will be acknowledged by any reflective mind. That this is true of other stoloniferous or rhizomatous plants horticulturists have experience in the strawberry. Leaves, and an occasional root, will sometimes appear from the apex of the common peduncle which some accident has bent in early stages to the ground. But a perfect illustration is seen in a variety known as the "Brush strawberry," which never makes any stolons or, as they are technically called, "runners," because, as is readily seen, what should have been runners in the usual varieties have become erect, and, with erection, have changed their character to flower scapes. The leaves are quite abundant among the flowers, and are on one side, as they are on the thick stemmed Begonias, and as they would be on a strawberry runner trailing on the ground.

It is evident that under the conception of a continuous spiral arrangement, the leaves, from a stem arranged for horizontal growth, could not all spring from one side as in the Begonias and other plants referred to; nor is there any method conceivable except that each leaf or bud in succession should be made to twist in contrary directions. We can see that this is so in the thick flowering shoots of the *Yucca filamentosa*, where the suppressed leaves, reduced to mere bracts, show the alternate twisting from right to left, and from left to right. (Fig. 1.) Examining the flowers on the branchlets of the panicle, we see that they also alternately twist in opposite directions, and that they are secund. In fact, the flower scape of this *Yucca* is but a rhizoma, forced to assume an erect position, changed in many of its characters by that unknown law which comes in a highly accelerated growth, and results in changing leaves and stem into inflorescence, although not wholly affecting the unilateral character that prevailed in its horizontal condition.

Fig. 1.

If we examine any cases of secund inflorescence, we may in most instances see that this condition arises from the alternate twisting of the pedicels in contrary directions.

So far as the author can now recall, the secund inflorescence, aside from that classed as scorpioid, does not exist among annuals, and we may assume that it is rare in that class. In perennial herbaceous plants it is common. Conceding that, as a general law, plants in time come to adapt themselves to the best conditions of existence, and that as a general law it would be better for leaves and flowers to be scattered equally around an axis than to be crowded on one side, the conclusion is rationally reached that a secund inflorescence is a comparatively recent stage in evolution, wherein a geotropic stem has assumed an erect condition.

Again, the author does not know that it has been so recorded by phyto-biological authors, but growth in plants evidently follows the law that prevails in most forms of motion, and is rhythmic and not continuous. Rest and activity follow in rapid succession as the parts of a plant grow. It is during these various stages of rest and activity that the successive morphological changes take place. It is probable that during these resting spells, the changes in the torsional direction occur. It has been shown by the author of this paper (see Proceedings of Academy, 1886, page 291) that after the resting spell that follows the expansion of some malvaceous flowers, they take the opposite direction in twisting as they close. The plants there noted are annuals, and the inflorescence is not secund. The alternate twists are in contrary directions, during successive resting periods in the same flower.

Noting that in an allied order a member, *Mahernia verticillata* had secund flowers, it was thought probable the expanding corolla itself, might show alternate twisting in contrary directions. This proved to be the case, the lower flower of the two twisting against the sun, and the upper with the sun. Fig. 2 represents a front-face outline, showing the opposite direction of the twists in the two flowers of the common peduncle. Notwithstanding the flower does not expand to the extent the malvaceous plants referred to above do, and the consequent difficulty the separate petals must have in changing the over-lap in fading, yet numbers succeed, showing that here also the return spiral twist is in a different direction and is not a mere coiling up of the same expanded spiral chain.

Fig. 2.

Distinct spiral directions in the growth of branches on the same plant have been occasionally noted (see Goodale Bot. Text Book, p. 407). The object of this paper is to show that it is very common in the inflorescence, and that it is indeed the cause of that section known as *secund*. The author would show that the inverse of Dr. Gray's definition of a stolon may be accepted. He says,—" A stolon is a prostrate or reclined branch which strikes root at the tip, and then develops an ascending growth, which becomes an independent plant." We now see that the stolon itself, with its unilateral arrangements, may again ascend and become a branch.

The author confines himself in this paper to those forms of scorpioidal inflorescence, that are not usually considered in connection with the subject, and which evidently occur by the twisting of the spiral growths. Those forms of unilateral inflorescence, more properly regarded as scorpioidal, and treated at some length in Gray's Botanical Text Book, Sixth Edition, page 163, would have to be examined from a different stand-point.

Note on Pinus pungens and its allies. Until comparatively few years ago, the Table Mountain Pine, *Pinus pungens* Mx., was not found north of the Potomac. Professor Porter found old cones at Huntingdon, Pennsylvania, and an aged local botanist at Bethlehem in the same State, told the author of this, that he had found old cones there. Since then the author found living trees in abundance at Port Clinton, subsequently in Dauphin County, near Harrisburg, and in January of this year near Lewistown in Mifflin County. It is safe to say it is found in the whole Allegheny range through the breadth of the State.

It is remarkable that a tree so widely scattered in this region should have been so long overlooked, and that the only person reported as having collected it in a living condition, should be the writer.

An interesting fact is that in all the Pennsylvania localities it seems to be found only in the upper Silurian formation

In the recently discovered Lewistown locality the rock is fossiliferous, being full of the casts of Brachiapodic shells. It is just possible it may reach the lower Devonian formation.

Another interesting point is that at Lewistown all five of the Pennsylvania species of the true Pines, are growing together: *Pinus Strobus, P. mitis, P. inops, P. rigida*, and *P. pungens*. *P. Strobus* and *P. mitis* make fine trees; some of the latter taller, and four feet in circumference.

One of the distinctive features of the species of Pine, and which cannot often be described among their specific character, is their habit of growth. By this they can be distinguished at a distance. *Pinus pungens* in this respect is seen to be more closely related to *Pinus rigida*, than to any of its neighbors. The side branches often branch and re-branch in *Pinus rigida*, taking on in this respect the character of a deciduous tree. Besides this the spurs, which in all pines are at the base of the fascicles of leaves growing towards the circumference of the branch year after year as the branch increases in thickness, but rarely getting far enough forward to form "secondary" leaves; in *Pinus rigida* manage in time to get beyond the bark of the main branches, again become foliaceous, and produce a dense annual crop of "needles" or secondary leaves along the whole surface. This has not been noted on *Pinus pungens*, though it has the character of making vigorous and much ramifying side branches more strongly developed. In many cases, the side-branches compete in vigor with the leaders, till the tree loses the specific character of most pines in having a distinctive trunk or leading stem, after it has reached no great height from the ground.

Another feature in which it agrees with *Pinus rigida*, is in the habit of bearing flowers, both male and female, on comparatively young plants. In the general characteristics of branches, foliage, and cones, it is easy to see the general relationship to *P. rigida.*

In one respect, however, there is a remarkable difference. *Pinus rigida*, is, in its cones, among the most variable of Pines. In his paper on "Variations in nature" read by the author of this before the American Association for the Advancement of Science, at its Montreal meeting, a series of cones was used in illustration showing a complete line between *P. rigida*, *P. serotina*, and *P. Tæda*, the changes being so gradual that, so far as the cones evidenced, no line could be drawn between the three, distinct enough as they are when the intermediates become "missing links." In the hills about Lewistown, some trees of *P. rigida*, were noted with cones little larger than good-sized Filberts. *Pinus inops* also varies very much in the form of its cones. But *Pinus pungens*, owing its parentage, as it probably does, to *P. rigida*, is remarkably constant in the size and form of its cones. Of the hundreds of trees that I have seen in the whole Allegheny range, from North Carolina to the Schuylkill river, the cones seem uniform in size and other characters.

In the unexpected appearance of a plant with which we are familiar in another region, we not only look for similarity in the geological features, but for companion plants as well. In the author's memory, *Polypodium incanum* is associated growing on rocks and trees with *Pinus pungens* in Virginia. It was natural to look for it here, but only its ally, *Polypodium vulgare*, was to be seen. It is possibly a low-land fern in its origin, pressing up into these higher regions long after the exposure of the Silurian rock in these upper elevations. At this dreary winter (January) season, the following few companions could only be noted :

Quercus coccinea, Q. Prinus monticola, Q. tinctoria, Juglans nigra, Carya tomentosa, Castanea Americana, Betula lenta, Acer rubrum, Ostrya Virginica, Rubus Canadensis, Rosa humilis, Juniperus Virginiana, Corydalis flavula, a wholly spineless *Cratægus* making a dense bush six feet high, *Danthonia spicata, Pycnanthemum muticum*, and numerous introduced plants that we expect to find everywhere.

On Corydalis flavula D. C. In January, in Pine woods near Lewistown, I noted some *Corydalis*, growing abundantly under *Pinus rigida*, and *Pinus Strobus*, plants of which I brought home, potted, and kept in a cool greenhouse. By the end of February they were in flower, and proved to be *Corydalis flavula*, D. C., *Fumaria flavula*, Rafinesque. Being able to watch their growth from day to day, I found a few points seemingly worth recording.

It is customary to say of this and allied species that the "racemes are opposite the leaves, or supra-axillary" (Torrey & Gray, p. 691) as describing that which is apparent. This is fair, but it is deceptive as to the actual fact. A raceme is but a branch arrested in its full axial development, and it is doubtful whether an axial growth, no matter what form of inflorescence it may assume, ever appears except from the axis of a leaf, or from the axis of the point where a leaf ought to be. To my mind it is a question as to whether every flower—each flower being regarded, morphologically, as an arrested branch—must not of necessity be terminal as regards its immediate axis; and whatever lateral direction it may subsequently assume, comes from a renewal of growth near or within the same axial line, the more or less horizontal positions assumed resulting by a pushing over, when the new axial growth is resumed.

That this is the case in this *Corydalis* is evident. The[1] raceme is at first a terminal spike. At its base is a leaf with an axillary bud. This bud, as it grows to a shoot, displaces the spike, assumes the central position, and the spike then becomes a "supra-axillary raceme," with the newly made axis, between it and the leaf to which it is axillary.

[1] Since this paper was prepared for publication the author notes that the raceme, so called, continues its growth to a number of nodes after the last flower has been produced, though the leaves at each node are still bractiform. Only for the fact that the leaves on the axis are reduced to mere bracts, it would be nearly as proper to say that the flowers are "axillary and solitary along the branches," as to say they are racemose.

An interesting fact is that at this node, where the terminal growth becomes a supra-axillary raceme, the petiole has assumed a sheathing base, and the two lower minute leaf blades are attached to the sheath in such a way that in ordinary cases we should be likely to conclude they were stipules. But we can see that the petiole of the normal leaf has been arrested in its growth, without affecting the laminal portion. It is as if an inch and a half of the normal petiole had been cut out, and a petiolar leaf rendered sessile. With this arrest of growth has come a tendency to dilation, resulting in the sheathing base to the leaf stalk. The observation is important as furnishing the key to other changes as the inflorescence advances in growth. Along the raceme are bracts, from the axils of which the flower springs. These are broad and oval, and in neither form nor texture like the laminal portions of the ordinary leaf. They are evidently formed by a dilation of the petiole, in the line of, and to a greater extent, than in the sheathing condition already noticed.

The fertilization of the flower is of peculiar interest. Mr. Darwin treats of *Corydalis* under the head of self-sterile plants (Cross-and Self-fertilization, chap. 14), though noting there that some species are occasionally self-fertile. This species as growing in my greenhouse, is fully self-fertile—not one flower failing to produce perfect pods and seeds. It is very interesting to observe the developing seed vessel, as it pushes through the maturing petal, carrying on its up-curved stigma a mass of white pollen, looking like a snow cap on the top of a green mountain. Examining the unopened flowers, we find that the pollen matures, and is actually placed on the stigma, long before the corolla has completed its growth—long before it is in any condition to receive the visits of insects. It is in fact as truly fertilized in the bud, as that class of apetalous conditions known as cleistogene flowers can possibly be. This can be readily understood by observing that in a raceme of ten flowers, the lower one only with the pistil having emerged from the closed flower, all but the two upper had pollen on their stigmas. It is a case in which the flowers are arranged for self-fertilization, with perfect productive results.

Dimorphism in Polygona. "Flores hermaphrodite," is said of the whole section of *Polygonaceæ* in which *Polygonum* is included; but though hermaphrodite they be, the hermaphrodism, so far as an examination of species growing near the author is concerned, is of a character hitherto unsuspected by botanists.

While preparing the chapter on *Polygonum arifolium* for *Native Flowers and Ferns of the United States* (1879, Vol. II, p. 154, series I), a double system of flowers was noted—one smaller than the other—but as both of them seemed to have the sexual organs perfect with anthers abundantly polliniferous, no reference was made to the fact, but the whole matter was laid over for future investigation.

Attention was drawn to the subject a few years subsequently, by noting numbers of nectar-loving *Vespæ*, as well as the common honey-bee vigorously at work on the smaller flowers of *Polygonum Virginianum*. These smaller flowers are pure white, and, after mid-day, expand sufficiently to expose the whole sexual organs to easy ocular examination. There are two series of stamens. The exterior lean outwardly, the inner bend inwards and the abundantly polliniferous anthers are in actual contact with the apparently perfect stigmas. The whole gynoecial system seems perfect. Those who speculate in these matters would surely say the flowers were specialized for self-fertilization. At the base of the inner series of stamens are glands which copiously exude nectar, attracting the insects above noted. It was evident, however, that none of these small, though apparently perfect, flowers, ever produced seeds. On the same plant are other flowers, larger, and of a greenish purple tint. From these flowers the styles with their hooked apices protruding, extend considerably beyond the sepals. These flowers always produce perfect seeds. Though the smaller flowers seem specialized for self-fertilization, in view of the fact that they produce no seeds, that they are abundantly nectariferous and polliniferous, and that the larger flowers project the pistils beyond the closed sepals, apparently out of reach of own-pollen, and yet are abundantly fertile, the general conclusion that the whole arrangement is for cross-fertilization would surely be pardonable.

During the several years past in which continuous observations were made, no insect has been noted visiting the fertile flowers. It is safe to say they are not fertilized by insect agency. The nectar in the infertile flowers doubtless serves some good purpose, but it certainly has no reference to cross-fertilization by insect agency.

Setting aside as wholly out of the question the production of nectar, and the visits of insects in connection with the fertilization of the productive flowers, it still remained to be considered whether the pollen, notwithstanding its sub-gelatinous character, might not be carried by the wind.

It was subsequently made clear that the pistils did not emerge from the floral envelopes till after fertilization had been accomplished. Indeed the seed had advanced considerably towards maturity before the styles were projected. It was only by the increased growth of the achenium following fertilization that the styles became exposed at all. The flowers are fertilized in the bud; there is no possibility of cross-fertilization. It may be remarked here, that the word "cross-fertilization" is used to express the pollination of a flower by another on the same plant. The physiological speculations involving questions of benefit to the plant or to the race, require the cross to be between different plants growing under separate conditions.

It was but natural to examine other Polygoni, in the light of the facts developed by *P. Virginianum*. The characters given were found in all cases, and still more strongly marked. These were the smaller, lighter colored, apparently perfect, flowers—expanding in the afternoon, gland bearing and nectariferous; abundantly polliniferous, but yet infertile. And there were the larger, colored, always-closed, and yet perfect flowers, resulting, without an apparent exception, in perfect seeds. In many cases the styles are bent in the bud, and the stigmas and anthers are brought together so as to make self-fertilization absolutely certain. Many are in fact truly cleistogamous. Occasionally with the growth of the fertilized achenium, as noted in the case of *P. Virginianum*, the remains of the pistils protrude through the floral envelopes, but this is not always the case.

In the light of so much that has been developed in connection with the relations between insects and flowers, these studies of Polygoni present an intricate puzzle. Here are all the facts, positively presented, required in the theory of cross-fertilization in this way. There is nectar, perfect pollen in abundance, and insect visitors. But there are no flowers to be fertilized. Those that are fertile—the only fertile flowers are absolutely closed to the insects,—are in fact cleistogamous.

The following is the list of species on which these observations are founded:—

P. orientale L.	*P. Pennsylvanicum* L.,
P. Persicaria L.	*P. Hydropiper* L.
P. acre, H. B K.	*P. Virginianum* L.
P. aviculare, L	*P. arifolium* L.

P. sagittatum L.

On the nature and office of Stipules. The author has printed a paper in the Proceedings of the Academy, 1870, pp. 114–117, on the Stipules of *Magnolia*, showing that the stipules not only performed the office of bud-scales, but that the petals were transformed stipules, and not metamorphosed leaves as we usually understand them to be. The good friend whose loss we all deplore, Prof. Asa Gray, generously examined the manuscript before publication, and expressed himself much pleased with the deductions drawn, observing, however, that if his memory served him right some German observer had before suggested that petals are occasionally but modified stipules. This is so obvious, that it would be surprising if the matter had not been discussed somewhere, but the author has never been able to discover the treatise that Professor Asa Gray believed he had read on the subject. It is safe to say that, as a general rule, stipules are not regarded as of any material importance in the economy of plant life. In the treatment of this subject they are simply spoken of as "appendages to the leaves," referred to as occasionally serving as a bud-scale, and then dismissed from consideration.

There is no essential difference between a stipule and the dilated base of a petiole. In some natural orders the presence of stipules characterizes every genus ; in allied orders the complete stipule may be wanting, but the bases of the leaves are widened and become thin. The leaves are then characterized as having petioles dilated at the base.

It is worthy of remark that in plants having dilated petioles the leaves with the petioles so dilated have much shorter petioles than those on the same plant not dilated ; in Ranunculaceæ and Umbelliferæ for instance. The same rule obtains in those genera where there is a difference in the size of the stipules in the same plant—some *Rosaceæ*. The size of the stipules is in inverse proportion to the length of the petioles. It is important to note that elongation is in a measure suppressed in proportion to the development of the stipule or the dilated petiolar base. This may be seen in the case of *Corydalis flavula* (see Contributions IV, page 58). It may also be noted in an examination of a stalk of clover, or a flowering branch of the rose. The stipules become larger and the petioles shorter as the flower bud is reached.

Exactly the same order follows the production of bud-scales, when a branch is about finishing its season's growth. Towards the end of the season the ends of the petioles widen ; the petioles themselves shorten ; and careful observations in many plants will show that the final result of this process is the bud-scale. When, again, the season for a renewal of growth occurs, the same process appears inverted. The small scale grows larger and wider. Often a perfect petiole is reached before a trace of leaf appears. In some species of Ash, and in the Dwarf Horse-chestnut (*Aesculus parviflora*), this transition is particularly evident. The result of the examination will clearly establish the fact that a bud scale is a transformed leaf to be sure, but a leaf in which the longitudinal growth has been arrested, and a quickened growth secured for the base of the petiole or stipule. We may more correctly say that a bud-scale is a transformed stipule, or dilated petiolar base.

Examining carefully the same growth-course in the clover or the rose, there is seen the same gradual modification. The stipules are enlarged until the leaf blades wholly disappear in the sepals ; the petals, still the same modified stipule, widen and enlarge. No other conclusion can be reached. But in the rose the sepals sometimes narrow, and the leaf-blade reappears at the apex. In some varieties grown in winter forcing houses, a perfect pinnate rose leaf appears. This is the case, notably, with a variety known to florists as Madame Ferdinand Jamain (in America " American Beauty.") Clear as it is to the mind that when carefully traced, the petal of a rose is formed of an enlarged stipule, and not of a fully planned leaf, the positive evidence is not furnished as freely as in the case of the sepal, but specimens of *Rosa humilis*, sent to me in 1883 by Miss Jennie E. Whiteside, of Harmonsburg, Pennsylvania, give an excellent illustration. This form has been figured and described by Mr. Sereno Watson in the *Garden and Forest* for February 13th, 1889 as *Rosa humilis*, var *triloba*. The trilobed petal is simply a case in which the usual stipule forming the petal of the rose, has again had its normal growth accelerated towards a perfect leaf. The central lobe is in fact no more than a dilated petiole, with the stipule represented by the two lateral lobes, in its normal position at its base. The same process from the total arrestation of petiole and leaf blade to the abnormal dilation of the stipule to form the petal, can be traced in magnolia, as made plain in the paper above cited.

When we come to formulate the general proposition that the bud-scales of branches, and the sepals and petals of flowers are modified stipules (or dilated bases of petioles), it will not be surprising if instances should be adduced where these organs are evidently modified leaf-blade rather than stipular. Nature seems so exhaustive in her efforts at variety, that though the morphologist should be able to prove his position in the greater percentage of cases, he learns, by experience, that "never" and "always" are dangerous terms.

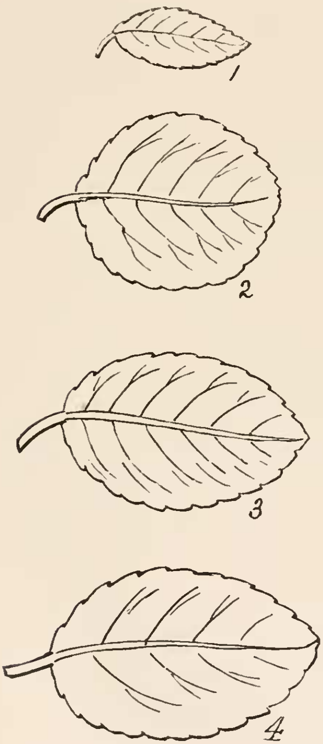
With this clearly conceived nature of bud-scales and floral envelopes before us, we get a nobler view of the office they have to perform in the economy of plant-life. We cease to look on them as mere "appendages" of so little account as to be usually dismissed with a few words in treatises on structural and morphological botany. They are the police force of vegetation, the defenders of the weak, the protectors of infancy in the vegetable world. From the scale of a Lily bulb, to the full-formed petal of the beautiful rose, we see the self-same chord with myriads of tones in perfect harmony. It is a good illustration of the unity of plan on which nature rings such varied changes.

And this conception of the nature and the office of stipules harmonizes the morphological conceptions heretofore prevailing as to the formation of the flower. We have long since ceased to say that a flower is modified leaves; we now teach that a whole branch is modified when nature undertakes to mould a flower. Now if we propose that bud-scales are modified stipules, and that their office is protection, when the organs of a branch are so modified as to produce a flower, the stipular conceptions should lead to protection also; and this is conceded to be the chief duty of sepals and petals. They are mainly for the protection of the tender parts they enclose.

Bud scales and the floral envelopes are modified stipules, and their office is protection to weaker portions of the plant structure.

On parallel habits in allied species from widely separated localities. In a paper published in the Proceedings of the Academy for 1862, page 10, the author of this paper pointed out that the variations in many allied species of Europe and America were always in the same line. For instance, if a European species had shorter internodes, larger buds, more serrate or thicker leaves, duller foliage in the fall, denser growth of branches than an American ally, species of other genera would also differ in the same comparative characters. In other words, the variations in character which distinguish the species of America from the species of Europe, are all on the same general plan.

It may now be noted that in two species of *Euonymus*—one of America and one of Japan—both remarkably dimorphic—the dimorphic one also has a remarkable correspondence. In our country we have *Euonymus Americanus.* L., which we sometimes find growing up as an arborescent shrub, of four or six feet, with a round head on a single stem of near two inches in diameter, and with thick, ovate, bright green leaves. At other times it is found as a low-trailing plant with thin linear-lanceolate pale green leaves, having, so far as I know, flowers but rarely in this trailing state. Many a young botanist, in his earlier experience, must have wondered, as the author has, whether they were not wholly distinct species. Riper years with accumulated knowledge of the range of variation, alone teaches the identity of the two.



Euonymus Japonicus, of Japan, presents the same conditions. This was long ago described by Thunberg under this name, and has been many years cultivated in American gardens. A leaf of this is given in Fig. 4. Laer has introduced *E. radicans* of Siebold, Fig. 1, representing a leaf of this form. For many years it was grown in our gardens as a simple low bush in shrubberies. Some plants growing near a low stone wall, took to climbing up as the well-known English Ivy or the American Trumpet creeper does, doing full justice to Siebold's specific name *radicans.* As soon as it reached the top of the wall, the leaves increased in size and general character, till it was difficult to trace any difference between them and *Euonymus Japonicus.* That they were dimorphic forms of one species admitted of no doubt. Cuttings of the upper branches with the enlarged leaves were made, but the young earlier branches pushing out from the cuttings, gave the true radicant form of Siebold, but eventually stronger branches pushed out with an erect habit. Fig. 1, 2, 3, are all graduated leaves from one of these plants. Fig. 3 will be seen to have reached very nearly the size and form of a true *E. Japonicus*, Fig. 4, but it is not quite so thick and shining.

As the two species are not distantly related, it is certainly interesting to note that the dimorphic one is of the same relative character in each case, the climbing habit being still wanting in the American species.

APRIL 2.

The President, Dr. JOSEPH LEIDY, in the chair.

Thirty-nine persons present.

The production of aerating organs on the roots of swamp and other plants:—The following communication was read from PROF. WILLIAM P. WILSON:—In the winter of 1885–86 I was in South Florida. While studying the plants about Lake Butler in Hillsborough Co., my attention was called to the excrescences on the roots of the bald cypress, *Taxodium distichum* Richard, generally called "knees." The water in the lake was very low. During high water the waves had washed bare the roots of many of the cypress trees along the shore. In this way an occasional tree was found whose earlier formed root-system was almost completely exposed.

These exposed roots offered excellent opportunity for the study of some of the points in the development of the so-called "knees." The very early stages were secured by digging up the complete root-system of young trees which were just beginning to show "knees," and also by cultivating at a later date seedlings under varying conditions. Some of the results early obtained led to the growing of other plants under varying conditions of moisture and dryness.

Certain points concerning the development and function of roots under the influence of excessive moisture, which seem to be clearly made out, will be very briefly stated in this paper. A more extended discussion of the same subject, including the anatomy of some of the roots with explanatory cuts will, I hope, soon follow in the Proceedings of this Academy.

Taxodium distichum produces whenever it grows in wet places, excrescences on its roots called "knees." These knees vary in size, in height and in number in accordance with the depth of water or amount of moisture existing under the trees. When the water for a part of the year is deep the knees grow correspondingly high. If the ground is simply overflowed and kept saturated with moisture most of the season these knees grow low but multiply themselves in great numbers. Fifty to one hundred may be produced from the root-system of one tree. If the overflow is considerable in depth the knees may exceed eight or ten feet in height. They are strictly root productions as will be shown later both by their development and anatomy.

The development of these knees is by two very distinct methods.

First, if the seed germinates and the plant begins its growth in a very wet place, many of the small roots which are only six or eight inches below the soil grow upward towards the surface at slightly varying angles of from 20° to 35°. Upon reaching the surface these same roots turn and go down into the soil at about the same angle. Some of them may, if the soil is very wet, or if under the water for a part of the season, repeat this method of growth several times in the course of six or eight feet. At each point where the root comes to the surface begins later the development on its upper side of the so-called "knees."

A remarkably rapid increase of cells on one side takes place at this point, which results in the constant elongation of the club shaped body, the knee. This point of growth I shall discuss in a following article.

The second method of knee formation takes place on old roots either horizontally or otherwise disposed to the surface. If the tree requires from inundation or other causes more aerating surface than can be readily or rapidly produced by young and growing roots, then either the whole upper surface of the root in question may become more active and rapid in its growth or the places of growth may be limited to certain definite points.

In the first case the whole root becomes widened, ribbon like and corrugated in general appearance. In the second, separate and distinct knees are formed. All knees cannot, however, be explained from these two simple methods. The cypress roots seem to have a very great tendency toward natural grafting. Whenever two roots cross each other and later through increase in diameter press upon each other they develop a natural union. In many cases when the ascending and descending part of the root which forms the basis of a knee approach parallelism they become later, through increasing diameter, wholly consolidated in the formation of the knee. It may happen that several knees begin their development within a few inches of each other. In such cases they may later become consolidated into one. The external parts of the knee above the soil in such cases may give little or no evidence of such consolidation. In the first mentioned method of knee formation the root passing from the tree to the "knee" is always less in diameter than the one leaving the knee. On the root descending from the forming knee there generally develops a cluster of roots, these often become consolidated later with the "knee." Roots which branch from the ascending part of the forming "knee" develop new "knees."

I do not propose at this time to discuss the function of these knees further than to say that their *location* and *occurrence* indicate beyond a doubt that they are for purposes of aerating the plant. Given conditions of sufficient dryness and plants of *Taxodium distichum* may be produced without a sign of these excrescences. The same or other plants may be placed under conditions of extreme moisture when after a time the "knees" will appear on both old and newly formed roots. The Taxodium seems to prefer swamps and inundated locations and in such places always produces the "knees." When cultivated in gardens and parks in dryer soils, where it readily grows, it never produces them.

The possibility of causing the development of these aerating organs in the cypress or, by changed conditions, of making them fail to appear at all, naturally leads one to examine other plants which from choice inhabit similar locations. There are numbers of trees and smaller plants which when flooded part of the season or grown in too wet soil will either form knees something like the cypress or send their roots up into the air above the water.

I have succeeded in causing common Indian corn to push up one or more roots from each plant above the soil by keeping the same saturated with moisture. Such roots grow up into the air and then turn downward and enter the soil, forming perfect knees for aerating the plant.

In Georgia on slopes remaining inundated during the wet season I have found the Pond pine, *Pinus serotina* Michx. making perfect knees on the water side something like the cypress, while the roots on the upper or dry side of the tree did not appear on the surface at all.

One of the most striking cases in which roots are sent up above the surface of the soil and water may be found in one of the sour gums the Water Tupelo, *Nyssa aquatica* L. of the Southern states. This tree sometimes grows in water holes associated with no other tree, thus resembling a Cypress head. I found such Tupelo-heads frequently in Georgia. In such cases the base of each tree was enlarged to double the diameter five to eight feet from the ground. Around the base of each tree extending six or eight inches above the high water line was a compact mass of roots, each one growing vertically up out of the water and after making a sharp bend growing down parallel with the upright part into the water again. There were sometimes dozens of these roots surrounding one tree closely appressed to its base. These roots varied in size from that of the finger to several inches in diameter.

The genus *Sonneratia*, and also *Avicennia* L. both furnish interesting trees which, growing in soils or ooze always saturated with water, have contrived to send up vertical roots for purposes of aeration.

Avicennia nitida grows in our own tropics and along the southern shores of Florida. These vertical roots which extend up above the soil from 6 to 10 inches are always in the air at low tide. They are covered with numerous lenticells through which the air enters the plant when they are not flooded.

There is no doubt but that all swamp plants and others growing between tide waters which are flooded during a part of the day have provided themselves in one way or another with means for root aeration. See interesting papers by K. Goebel[1] L. Jost,[2] and Shaler.[3]

The following were ordered to be printed:—

---

[1] Berichte der deutschen botanischen Gesellschaft, Jahrg. 1886, S. 249.

[2] Botanische Zeitung, Nr. 37, 38 u. 39—1887—S. 601.

[3] Memoirs of the Museum of Comparative Zoology at Harvard College, Vol. XVI. No. 1, June 1887; Science, Vol. XIII. No. 318 p. 176.